# CONTRIBUTIONS TO THE FLORA OF NOVA SCOTIA. IX. HABITAT STUDIES OF ARCTIC-ALPINE AND BOREAL DISJUNCT SPECIES<sup>1</sup>

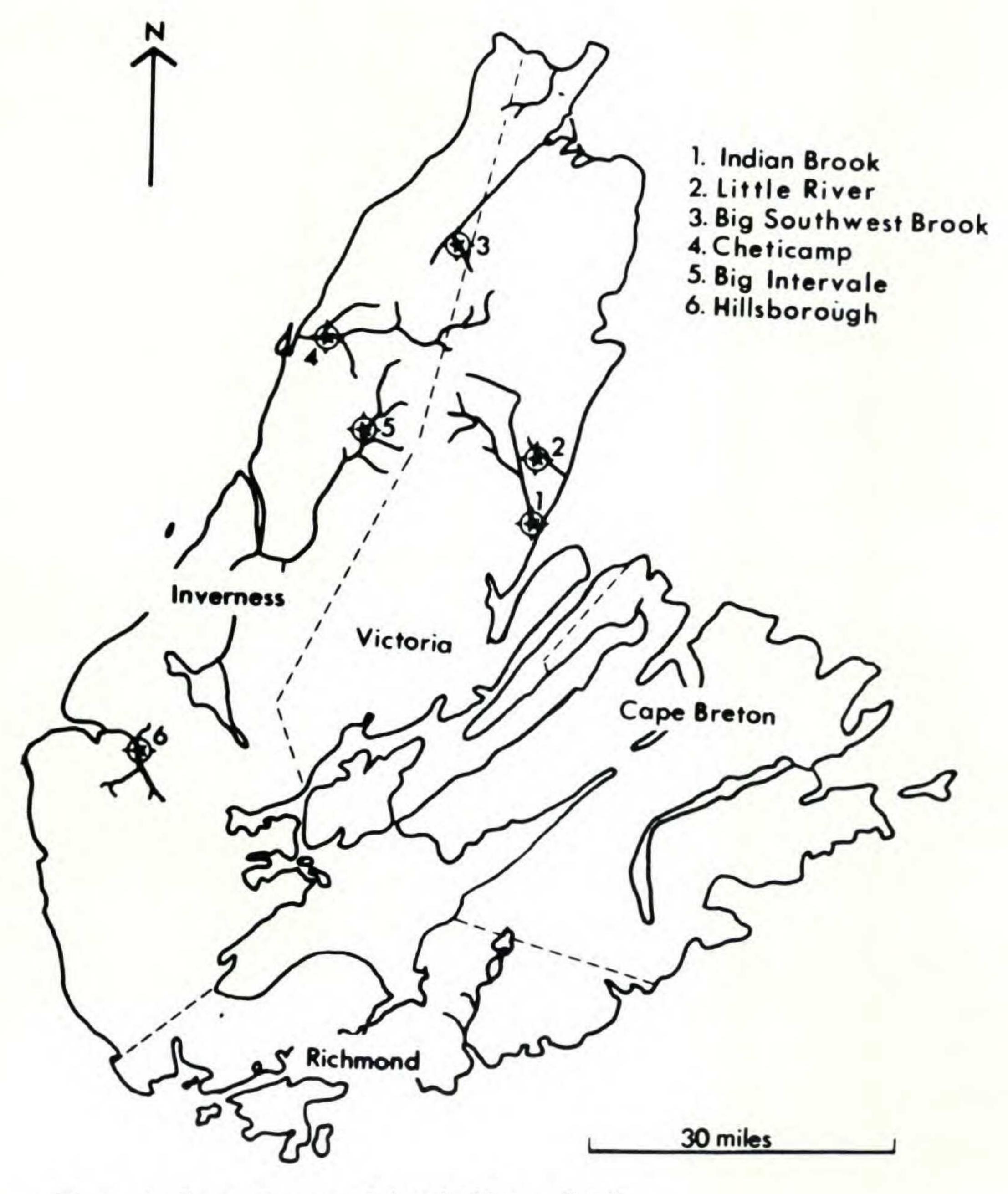
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The flora of Nova Scotia contains many species of disjunct distribution. In the southwestern section of the province are found species that are usually associated with the Atlantic Coastal Plain of the United States. Roland (1947) discussed this element, listing such species as Rhexia virginica L. and Woodwardia aerolata (L.) Moore. In recent years exploration in northern Cape Breton by the junior author and his forest ecology field crews from Acadia University has resulted in a growing list of species with northern affinities (e.g., Smith and Schofield, 1952; Smith and Erskine, 1954). That these Arctic-alpine and boreal disjunct species have two centres of distribution in Nova Scotia (viz. the northern Cape Breton area and the Minas Basin-Bay of Fundy area) was shown in a previous paper (Hounsell and Smith, 1966). The aim of the present paper is to describe some of the small, isolated stations harboring these species and hence to shed some light on the twin problems of their disjunction and persistence.

Northern Cape Breton Island comprises a region of highlands surrounded by a narrow coastal plain which accommodates a highway known as the Cabot Trail. This road links the seaside villages but makes few incursions upon the inland and upland wilderness about one half of which is within the Cape Breton Highlands National Park. Although the terrain rises but little above 1500 feet it is dissected by many narrow, steep river gorges where the bog-fed rivers that originate in the flat, central uplands channel their way to the coast. The sheer wet cliffs found at the many water-

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Map of Cape Breton Island, Nova Scotia

falls and at other points along the gorges provide suitable habitats for Arctic-alpine and boreal disjuncts.

Practically every river valley examined to date has been shown to possess one or more disjunct stations, none of which is very extensive in size; some are a few hundred yards long, others much smaller. Some provide an acceptable niche for only one species, but most harbor several. Of the 58 species included in this study the largest number

found at one station is 27, at Big Southwest Brook. Lock-hart Brook, flowing into the Salmon River, follows closely with twenty-five. These two stations are by far the richest in species number.

In an attempt to determine those environmental factors that have allowed the relic northern flora to survive in isolated pockets, presumably for 8,000 years or so, a study was made of the habitats at six stations in northern Cape Breton (Fig. 1) in the summer of 1964. Each station consisted of a river-valley cliff-face with its associated talus slope. The talus and that part of the cliff which was accessible were examined both for vegetation and variation in habitat. A species list was made for each small detectable change in habitat and the relative commonness of each species was noted, not only for disjuncts but also for those species of the surrounding forests, river gravels and fields that had been able to invade the cliff habitat. Rock and soil samples were taken at each site for later analysis. Note was made of the extent, sheerness and stability of the cliff and talus, of degree and direction of exposure and of seepage.

## (A) INDIAN BROOK, VICTORIA COUNTY

The Indian Brook station is located on the south side of the stream about one half mile west of the Cabot Trail at a river elevation of 50 feet above sea level. Nichols (1918), in the course of his study of the vegetation of northern Cape Breton Island, travelled extensively in this general area and collected a number of disjuncts but made no reference to this small but rich colony; it was not until 1952 that this station was discovered.

Indian Brook runs through a deep gorge whose steep sides rise, in steps, at least 200 feet, often from the very edge of the stream. The cliffs are not continuous but interrupted by steep wooded slopes such as those which flank the disjunct station.

A fan-shaped talus slope extends from the river's edge up to a sheer cliff which rises about 70 feet beyond the talus. A dike on the east side and a deep chimney-like crevice on the west side separate the main part of the cliff from two adjacent sections. The bases of these side cliffs slope downward from the top of the talus until they reach to within a few feet, vertically, of the summer water level at a horizontal distance of 30 feet from the river. All three sections of the cliff are mainly north-facing but the eastern section has a considerable extent of west-facing surface. The horizontal measurement of the cliff is approximately 220 feet.

Above these cliffs the forest extends up the steep and terraced slope to the relatively flat area above the gorge. On each side the forest descends practically to the water's edge but bands of herbaceous vegetation, growing among boulders that are water-covered in the spring, separate it from the river.

Near its base at the spring water level, the talus measured 56 feet across and consisted mainly of boulders, two to three feet long, that had once been part of the cliff. Between these partially weather-smoothed boulders small pockets of soil have accumulated, possibly through filtering from above, supporting a sparse but varied strip of vegetation. Among the herbaceous plants seen were Satureja vulgaris (L.) Fritsch, Carex intumescens Rudge, Thalictrum polygamum Muhl. and Taraxacum officinale Weber. All of these are common constituents of the Nova Scotian flora.

In the finer, less stabilized talus, farther up the slope, occurred such common plants as Anaphalis margaritacea (L.) C. B. Clarke var. intercedens Hara, Achillea millefolium L., Hieracium pilosella L. and Solidago flexicaulis L. On the talus, as well as on the sheerest of faces, was found Campanula rotundifolia L.; this proved to be one of the commonest plants at all the stations visited.

The main, north-facing cliff is sheer but broken by numerous small crevices and cracks. At the time of visiting most of it was extremely dry; only near the base where the rock is much fractured and crumbled was there evidence of seepage. In this section, in rather dry pockets of soil on narrow ledges, two boreal disjuncts, *Arabis hirsuta* (L.)

Scop. var. pycnocarpa (M. Hopkins) Rollins and Draba arabisans Michx., were noted. Saxifraga aizoon Jacq. var. neogaea Butters, an Artic-alpine species, was also collected from this cliff section.

A soil sample taken from a deep pocket at the cliff-base had a pH of 6.9. The exchangeable calcium and magnesium were both comparatively low (Table I).

TABLE I

ANALYSES OF SOIL SAMPLES

(Ex. Ca. — exchangeable calcium in M. eq.; Ex. Mg. — exchangeable magnesium in M. eq.)

STATION	рн	EX.	EX.	REMARKS
INDIAN BROOK "A"	6.9	1.60	0.34	Crevice at base of sheer cliffs, above talus.
INDIAN BROOK "B"	6.1	1.00	0.22	Moss-mat, sloping cliff, with Saxifraga aizoon var. neogaea.
INDIAN BROOK "C"	6.3	7.89	2.70	Dry cliff ledge — Draba arabi- sans and Arabis hirsuta var. pycnocarpa.
LITTLE RIVER	6.5	3.02	1.55	Ledge in damp grotto.
BIG SOUTHWEST	3.8	0.89	1.64	Dry, grassy west-facing ledge with Carex capillaris var. major.
BIG SOUTHWEST	5.6	5.08	5.20	Wet ledge below main cliff, east-facing, Scirpus cespitosus var. delicatulus.
CHETICAMP	5.9	2.85	4.65	Wet, north-facing ledges, Achil- lea borealis, Scirpus cespitosus var. delicatulus.
BIG INTERVALE	4.6	3.58	6.20	$\begin{array}{l} {\rm Dry\ ledge} - Arabis\ drummondi, \\ Woodsia\ ilvensis. \end{array}$
HILLSBOROUGH	7.3	9.08	1.55	$\begin{array}{lll} {\rm Limestone} & {\rm cliff}-Cystopteris\\ bulbifera, & Cryptogramma & stelleri. \end{array}$

Fine talus, harboring no disjuncts, covers the floor of the slanting dike that serves as the eastern delimitation of the

main cliff. Immediately to the north of the dike the eastern cliff of the three-parted complex has a small face exposed to the northwest and a more extensive, almost vertical face exposed to the north. The northwest face has a slope of about 45 degrees. Seepage was evident on the bottom half, leaving the upper section dry and practically devoid of plant life. Low moss mats and crustose lichens covered much of the moist section of the unbroken rock surface. Saxifraga aizoon var. neogaea was the only vascular plant present in the limited anchorage and soil available.

A soil sample taken from the moss-Saxifraga mat was later found to have a pH of 6.1. Exchangeable calcium and magnesium were both low. Rock taken from this cliff section was identified as syenite — an acidic rock with feldspar and probably mica.

Grassy ledges of the western cliff supported, in addition to wide-ranging species such as Campanula rotundifolia and Hienacium canadense Michx., patches of disjuncts, including Draba arabisans, Anabis hirsuta var. pycnocarpa, Woodsia ilvensis (L.) R. Br., Poa glaucantha Gaudin, and Achillea borealis Bong. These grew on exposed, dry ledges which received much shade from small trees that had, here and there, gained a foothold. Cystopteris fragilis (L). Bernh. var. laurentiana Weath., a boreal disjunct, occurred frequently in the lower crevices but the commonest occupant of the basal, seepy areas was Woodsia ilvensis which was able to thrive in the tiniest of niches. A soil sample taken from a narrow ledge that supported Draba anabisans and Arabis hirsuta var. pycnocarpa was found to have a pH of 6.3 and correspondingly low values for exchangeable calcium and magnesium. Both of these species have been described as calcicoles by Scoggan (1950) and others but here they are found in the soil with much less calcium and a lower pH than they seem to prefer in Gaspé and Bic.

The lower section of the western cliff is quite different from the more exposed, mainly dry upper half described above. It is about 30 feet high and 85 feet long, set back 40 feet from the summer water level and 15 feet above it. Large deciduous trees growing between it and the river provide continual shade during the summer. The upper 20 feet of the sheer cliff is relatively dry, supporting but a few mosses and lichens but throughout the lower ten feet seepage was extensive, soaking the crevices and ledges and forming small pools in the basal grottoes.

Because of the deep shade and the continual supply of water this habitat was much cooler than those of the surrounding, more exposed and drier cliffs. Woodsia ilvensis, W. glabella R. Br. and Asplenium viride Huds. were common in the very wet grottoes, while Carex atratiformis Britt., Arabis hirsuta var. pycnocarpa and Achillea borealis were fairly common ledge - dwellers, all being disjunct species. Sedum rosea (L.) Scop., which is found well into the Arctic regions but is also known from many stations in Nova Scotia, was common on the almost vertical walls, growing out of very small cracks. Another common plant was Erigeron hyssopifolius, Michx., a boreal and alpine species.

Among the plants which occurred at the lateral edge of the lower half of the talus, where stablization was well advanced, were several which, while not disjuncts, are still of interest as pioneers on talus slopes. Aralia racemosa L. and Rhus radicans L. var. rydbergii (Small) Rehd. (two calciphytes) were common as was Ribes hirtellum Michx., while Dryopteris marginalis (L.) Gray and Polystichum braunii (Spenner) Fee var. purshii Fern. were somewhat less frequent. Other pioneers included Hieracium pilosella, Sambucus pubens Michx., Epilobium glandulosum Lehm. and Diervilla lonicera Mill.

In all 15 disjunct species have been found at the Indian Brook station, occurring in open or sheltered locations. The little ferns, Asplenium viride and Woodsia glabella, were restricted to wet, shaded, sheltered crevices and grottoes. On the drier exposed ledges were disjuncts such as Draba arabisans and Achillea borealis together with common and weedy species. Saxifraga aizoon var. neogaea persisted on

an exposed, inclined face in acidic soil on acidic rock although it is known as a calciphyte. All three soil samples from this station were slightly acidic.

# (B) BIG SOUTHWEST BROOK, INVERNESS CO.

Big Southwest Brook is the main tributary of the North Aspy River which it approaches from the south-southeast. The disjunct station is situated about 1/3 mile upstream from the river, approximately in the centre of the Cape Breton Highlands National Park. The elevation at this point is about 1,000 feet.

To the south the station is delimited by a waterfall, 60 feet high, which tumbles through an extremely narrow and crooked gorge (three to four feet wide in places) into a deep pool below. High cliffs encircle the pool but leave a small rocky bar on the northeast side. Upon leaving the pool the brook runs through a deep, rugged, boulder-strewn gorge. Many of the boulders are 15-20 feet across.

Arctic-alpine plants have been found along cliffs of this brook from the falls to a point approximately ¼ mile downstream. The narrowness of the deep trench through which the brook runs, combined with the orientation of the cliffs, puts the entire station in almost continual shade.

The west wall of the waterfall's narrow channel swings away from the falls to form a huge cliff that towers above the pool. Up to 100 feet high and 120 feet wide at the base this almost sheer cliff is criss-crossed by sloping ledges several feet in width. Wooded hillsides continue upward from the cliff top and also form the northern boundary of this section of the extensive but broken station.

A small pile of rock fragments that obviously had fallen from above was noted in the water at the cliff base but on the whole this face appeared to be fairly stable. Numerous horizontal fractures gave the cliff a stratified appearance. Schist, associated with banded gneiss and white milky quartzite, constitutes the major part of the cliff. Schist, gneiss and quartzite are all acidic rocks; the pH of a soil sample taken from a crevice of this face was 5.6. It should be pointed out here that this cliff previously was thought

to be composed of limestone (Smith and Schofield, 1952), an assumption that seemed quite plausible in the light of the number of calciphytes found upon it.

The entire cliff was extremely wet; water dripped everywhere and in some places it fell down the face in small, continuous streams. Spray from the falls helped to moisten the rock walls but it was chiefly the abundant seepage that created this very wet habitat.

At 0715 hrs. 29th July, the sun first shone on part of the higher region of the cliff, but 30 minutes later shade enveloped the whole face. Other sections of the east-facing cliffs received only a little more direct sunlight. The lack of direct sunlight plus the copious supply of dripping water made these cliffs considerably cooler than the drier, sunlit ones on the east side of the brook.

The commonest species on the waterfall cliff was Scirpus cespitosus L. var. delicatulus Fern., a boreal disjunct, followed by Sedum rosea, an Arctic-alpine plant, and Thalictrum polygamum. The first of these three was by far the most common, pioneering the smallest of cracks on the sheer facade. On the many ledges grew other disjuncts, including Erigeron hyssopifolius, Cystopteris fragilis var. laurentiana and Saxifraga aizoides L. Also common was Potentilla fruticosa L., a species which ranges into the Arctic but is wide-spread in Nova Scotia.

Downstream from the waterfall cliff are other lesser cliffs and overhangs providing habitats for still more disjuncts. Schizachne purpurascens (Torr.) Swallen, Woodsia glabella, W. alpina (Bolton) S. F. Gray, Solidago multiradiata Ait., Draba norvegica Gunn, Carex atratiformis, Arnica chionopappa Fern. and Achillea borealis were all found in small numbers scattered along the cliffs of this gorge. Pinguicula vulgaris L., a species previously unknown for this station was discovered in a wet crevice of a ledge projecting out into the river; only two plants were seen despite a close search. This small population and its dangerous position in time of floods is illustrative of the precarious existence of many of the disjunct cliff-dwellers.

More Arctic-alpine and boreal disjuncts were found at Big Southwest Brook than at any of the other stations studied. It is the only known Nova Scotian station for *Draba* norvegica, Saxifraga aizoides and, above the falls, Oxyria digyna (L.) Hill.

The western half of the station generally was wet, well-shaded and thus cool while the opposite cliffs were exposed to sunlight, drier and therefore warmer. The number of disjuncts on the western side was greater, both for total number of species and for total number of plants. The dissimilarity of the two sides is most vividly seen at the falls where the falling water divides the encircling cliff into two distinct vegetational sectors; to the west it is shaded, wet and covered in a lush profusion of higher plants, to the east it is sunlit, dry and covered in lichens. Soil samples from both sides were acidic but the eastern sample was much more acidic than the western.

## (C) CHETICAMP RIVER, INVERNESS CO.

One and a half miles southeast of the point where the Cabot Trail crosses the Cheticamp River a steep mountain rises from the south side of the narrow intervale which is but 100 feet above sea level. The western, northern and eastern sides are all very steep but on the south, the top becomes continuous with the flat plateau. An elevation of 1250 feet is reached at the very top, but the cliffs examined had their bases at about the 1000 foot level.

Cliffs encircled much of the topmost region of the mountain with extensive scree beneath them. Some areas were covered by a bare talus, mostly of boulders up to ten feet across. A visit to the station a year after this study was made revealed that almost 1/3 of the former suitable habitat had been swept away by a large slide.

All of the cliff sections investigated were approximately north-facing, very much exposed and usually moist. The first area examined was one of moist dripping cliffs which were quite steep but interrupted by ledges. These ledges were very mossy, supporting Sedum rosea and Potentilla fruticosa. A wet crevice near the base contained Scirpus

cespitosus var. delicatulus and Lycopodium selago L. Primula mistassinica Michx., a boreal-alpine, was frequent on moist ledges near the base.

The second cliff section studied was north-facing and very wet also. Water was continually dripping from the higher regions of the cliffs, splattering on ledges below and finally reaching the ground as a fine spray. When this station was visited the cliff-face habitat was considerably cooler than the intervale below. The slightest breeze was able to blow the falling spray over a wide area of the cliff. Shade provided by the mountain itself prevented rapid evaporation.

A pH of 5.9 was found for a soil sample taken from one of the wet north-facing ledges which supported, among other species, *Achillea borealis* and *Scirpus cespitosus* var. *delicatulus*. The major rock constituent of the cliff proved to be gneiss (an acidic rock), containing quartz, mica and feldspar.

Of the 58 disjuncts considered in this study, eight have been recorded for this Cheticamp River station. Almost exclusively they are found on moist ledges or in damp crevices that abound on the shaded, exposed dripping cliffs.

# (D) BIG INTERVALE, INVERNESS CO.

A relatively small disjunct station is located opposite the village of Kingross, on the west bank of the Northeast Margaree River where the river valley widens to form what is known as the Big Intervale. The elevation at the base of the cliffs is approximately 500 feet.

Facing south-east, the cliffs are generally bare and dry, exposed to both the sun and the elements. Scree, stabilized by numerous mature trees, slopes down gently from the cliff base to the flat hay-fields about 50 feet below. The cliffs extend laterally for about 300 yards but are only 50 feet high, at the maximum.

Much of the rock is covered by lichens only but the many ledges enable a number of species to prosper. Most are common weedy species from the fields or from the surrounding forest but ten disjunct species have been recorded for this small station. On the dry, mossy, exposed cliff *Achillea borealis*, *Woodsia ilvensis* and *Arabis drummondi* Gray have been able to persist. A small rivulet near the centre of the cliff-face provided the only similarity between this station and the wet, cool shaded habitats of the three stations described previously.

The pH of a soil sample taken from a dry cliff ledge where *Arabis drummondi* and *Woodsia ilvensis* were growing, was 4.6. Rock from this face was described as igneous, probably syenite, which has been highly faulted and fractured. This type of rock is acidic.

# (E) HILLSBOROUGH, INVERNESS CO.

On the steep east bank of the Mabou River, one and a half miles upstream from Hillsborough, sheer outcroppings of limestone provide a type of habitat seldom found in Nova Scotia. In the limited area studied — a section of cliff about 60 yards wide by 15 feet high — seepage and small trickles were common, resulting in a generally damp cliff-side. Despite the wet, cool, fairly well shaded habitat only one disjunct species occurs there — Cryptogramma stelleri (Gmel.) Prantl. This species, a calciphyte, is known from only one other station in Nova Scotia. Among the non-disjuncts seen were two other calciphytes, Cystopteris bulbifera (L.) Bernh. and Sphenopholis intermedia Rydb.

## (F) LITTLE RIVER, VICTORIA CO.

The cliffs at Little River, about two miles from the Cabot Highway, had not been visited previous to the study. The site was selected at random with the hope that it would present an example of an exposed granitic cliff much similar physically to the disjunct stations. Such was the case. No Arctic-alpine or boreal disjuncts were anticipated on these high cliffs which terminate a long gradual slope from the intervale far below. Part of the lower slope was covered by a huge slide of boulders which evidently had broken from the faces above at some much earlier date since lichens and mosses had become well established. The cliffs were approximately 500 feet above the river level which at this point was 300 feet above sea level. Those faces examined

were from 30 to 50 feet high but were much more extensive laterally.

In general the cliffs were dry and bare but some of the ledges provided anchorage for several species. Trees growing in the stabilized talus gave a measure of shade.

Four disjunct species were found at Little River. Asplenium trichomanes L., boreal circumpolar in distribution, occurred frequently on the talus slopes and on the boulder slide. Dryopteris fragrans (L.) Schott var. remotiuscula Komarov was collected from a small crevice of the sheer cliff. Lycopodium selago was fairly common in soil pockets of some of the ledges and Woodsia ilvensis appeared to be a pioneer in bare areas. All four were found in slightly acidic soil. None of the really rare disjunct species were seen at Little River.

Soil preferences of a large number of Alpine and subalpine plants were discussed by Fernald (1907). Precipitation and moisture were considered to be of only minor importance in determining the local distribution of these plants in areas south of the St. Lawrence River. A correlation was seen between the distribution of certain species and the presence of limestone and other calcareous rocks. The role of exchangeable calcium in the soil was examined by De Silva (1943) in a study of the distribution of calcicoles and calcifuges. He noted that species which show luxuriant growth on calcareous soils often grow well in soils which appear to have no calcium carbonate whatsoever. Exchangeable calcium was postulated to act as a source of calcium in areas devoid of calcium carbonate.

With the exception of the limestone cliffs at Hillsborough, the stations examined in this study have acidic rock, pH's varying from slightly acidic to strongly acidic and low amounts of exchangeable calcium and magnesium. Most of the species considered here have been described as calciphytes and in the past the local occurrence of such species has often been explained on the basis of calcareous outcroppings. From the present data it would appear that

these plants can also persist where the soil is non-alkaline and even strongly acidic.

Wynne-Edwards (1939) elaborated upon the significance of the type of habitat wherein the Arctic-alpine species chiefly are found. Arctic plants are adapted to exposure and to habitats which undergo great physical change due to the actions of frost and thaw. To the south somewhat similar habitats exist on mountains, cliffs and talus slopes. Those cliffs composed of rocks which yield most easily to the process of weathering come close to resembling, physically, the Arctic habitats. The normal, mesophytic species find such conditions very difficult and often succumb to the competition of the better adapated Arctic-alpine element. The author pointed out that since basic rocks are more pervious and more soluble than acidic rocks they are more easily broken down by the weathering agents. In this way an ever-receding cliff-face and an unstable talus slope are made available to those species which are tolerant of changing, exposed habitats.

Although none of the six stations other than Hillsborough had cliffs of basic rock there was loose rock or talus below all of them. The most stable was probably the main cliff at Big Southwest Brook but even that was much fractured. It seems, then, that acidic cliffs can also provide unstable habitats.

The possible role of microclimate in plant distribution has been discussed by Wolfe (1951). Within the macroclimate of a region there is a complex pattern of microclimates operating just above the substrate and, in some cases, varying considerably from the norm of the region. Wolfe presented climatic data which showed that the maximum temperature for a certain grotto was 18 F. degrees below that of the surrounding countryside. It seems probable that the cooler temperatures of such a shaded habitat could promote the growth of Arctic species which might otherwise fail to survive. Although no temperatures were taken during this study the effect of shade and moisture

was sufficiently pronounced that valid comparisons could be made.

The most productive stations of the six visited in the present project were those which enjoyed the greatest amount of shade and shelter, Indian Brook and Big Southwest Brook. Of the 58 disjunct species 27 were recorded for Big Southwest Brook and 15 for Indian Brook. The cliffs at Cheticamp were moist and cool but were not as sheltered and did not receive as much shade. It is also possible that the almost constant winds at this higher, more exposed site led to faster evaporation. These factors may well in part account for the fact that only 8 species were found on the Cheticamp cliffs.

The Big Intervale station was exposed, very dry and faced southwest. Here only three disjunct species were seen, although in its one hundred years as a known station a total of ten have been reported; perhaps some have failed to survive due to the dry, unshaded environment. The cliffs at Little River were high, exposed, east-facing but quite dry. Only four disjuncts were found there. Although the limestone cliffs at Hillsborough were very moist and fairly well shaded they harbored but one of the 37 disjuncts.

A common denominator for the three most productive stations of this study is a cool habitat. In each case trickling and seeping water was present in varying amounts, moistening the shaded cliffs. The water and the shade are probably not ends in themselves, important though they may be; it is likely that their most important function is in contributing to the coolness of the habitat. The temperature-moderating effect of a river running by a cliff, in combination with shade and seepage, could well be a telling factor in determining the suitability of the habitat for Arctic-alpine species.

While the cool, moist habitat is of great importance it cannot guarantee the presence of disjuncts. If such were the case many of the river valleys and gorges would constitute continuous stations for the Arctic-alpine element. The edaphic and physiographic nature of the habitat also

help to determine which plants will grow there. Exposed, unstable habitats of cliff-faces and talus slopes make the establishment of an individual and the persistence of its progeny very hazardous. But it is on these moist, cool, relatively unstable habitats that the Arctic-alpine element can best compete with the flora of the surrounding areas.

Such habitats are fairly common in northern Cape Breton, present to a lesser extent in the Minas Basin-Bay of Fundy region but only rarely found in other regions of the province; hence, the bicentric pattern of distribution.

Immediately following the retreat of the Wisconsin glaciers the whole of Nova Scotia probably offered habitats suitable for the northern species which, previously, had been pushed south. In the warm period that ensued mesophytic flora took over most of the lowland sites, restricting what are now disjuncts to the cooler localities which were physiographically still pioneer habitats. There the mesophytic flora was at a competitional disadvantage such that the northern species were able to persist although much reduced biotypically due to the rigours of forced migration.

#### SUMMARY

The peculiar combinations of shade, moisture, temperature, exposure and instability of habitat allow isolated colonies of Arctic-alpine and boreal disjuncts, each typically consisting of a number of species, to exist as biotypically reduced remnants far from the present population centres. These same factors militate against most of the species of the surrounding forest so that the isolated populations can compete on at least an equal basis, thereby maintaining their precarious hold. A minor change in the habitat could swing the competitional balance in the direction of the common species with the almost inevitable elimination of these outliers.

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